

Female colour polymorphism in damselflies: failure to reject the null hypothesis

OLA M. FINCKE

Department of Zoology, University of Oklahoma, Norman, OK 73019, U.S.A.

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Abstract. The adaptive significance of colour polymorphisms in adult females within the Odonata remains controversial. Proposed benefits for male-like andromorphs include increased reproductive isolation and/or decreased harassment from conspecific or heterospecific males. Proposed costs balancing such benefits are increased predation on andromorphs, and/or failure of andromorphs to mate at low male densities. Nevertheless, data from past studies are insufficient to reject convincingly the null hypothesis that colour polymorphisms are neutral with respect to natural or sexual selection. Long-term data on two species of *Enallagma* damselflies are presented that are consistent with the null hypothesis. Male responses to tethered females suggested that males more readily recognize the most abundant morph as 'female'. Nevertheless, the two colour morphs did not differ in the time of day that they were seen in tandem, daily or lifetime mating frequency, life span, oviposition duration, inter-clutch interval, or maturation rate. These results indicated that male discrimination between morphs was predictive of neither costs nor benefits of the polymorphism in terms of female reproductive success.

Within the Odonata and especially within the damselfly family Coenagrionidae, sexually mature females of many species exhibit colour polymorphisms (Tillyard 1917; Walker 1953). Typically the body coloration (but not necessarily pattern) of adult 'andromorphs' (or 'androchromotype', Hilton 1987) resembles that of males, whereas that of 'heteromorphs' differs considerably from the male's (Johnson 1964). Coloration of mature females has been found to be controlled by one to two genes. The andromorphic allele is recessive in *Ischnura damula* and *I. demorsa* (Johnson 1964, 1966) but dominant in *I. graellsii* (Cordero 1990a). Although immature females also may exhibit developmental colour changes that signal their receptiveness to males, and sexually mature andromorphs may change into heteromorphs (e.g. *I. verticalis*, Fincke 1987), I focus here on colour polymorphisms that do not change after females mature sexually.

Several authors have proposed that female polymorphisms are selectively maintained by a balance of costs and benefits to each morph. Two relative advantages that have been proposed for andromorphic females are more effective reproductive isolation (Johnson 1975; De Marchi 1990) and reduced harassment of mated females by

males ('male mimicry hypothesis', Robertson 1985; 'density-dependent hypothesis', Hinnekint 1987). Two costs proposed to balance such advantages are greater predation risk to the purportedly more conspicuous andromorph (Johnson 1975; Robertson 1985) and/or failure of andromorphs to mate at low male density (Hinnekin 1987). This latter cost was first proposed for female butterfly morphs that mimic unpalatable heterospecifics (Vane-Wright 1980, 1984), but because no odonate is known to be unpalatable, Vane-Wright's hypothesis for the maintenance of the dimorphism is unlikely to be applicable to odonates. Stamps & Gon (1983) hypothesized that colour polymorphisms are limited to the female sex because sexual selection on male coloration overrides the benefits to males of being cryptic. However, because thorax and abdomen coloration of coenagrionid damselflies is not known to function in either male-male competition or female choice, this hypothesis is not applicable to this family, where polymorphism is limited to body coloration.

Alternatively, coloration of odonate females may be a selectively neutral character whose frequency varies among populations as the result of founder effects and random genetic drift

(hereafter termed the 'null hypothesis'). Although equal lifetime fitness of the morphs is consistent with both the null and the adaptive hypotheses, the null hypothesis predicts no differences between morphs in fitness correlates (e.g. survivorship and mating efficiency) despite fluctuations in male or female density, morph frequency, or the operational sex ratio. In contrast, the adaptive hypotheses predict that fitness correlates differ between morphs but are balanced at an equilibrium frequency, either by fixed trade-offs in fitness correlates between morphs, or by fluctuating fitness of the morphs. For example, relative to heteromorphs, andromorphs may consistently have greater mating and/or oviposition efficiency but lower survivorship (Johnson 1975; Robertson 1985). Or, as proposed by Hinnekint (1987), the mating efficiency of andromorphs may be higher than that of heteromorphs at high male density but, because males are always less likely to recognize andromorphs as potential mates, at low male density, andromorphs may be more likely to remain unmated. Alternatively, if males more readily recognize the majority morph as 'female' (herein) and, consequently, the minority morph enjoys relatively greater mating efficiency as long as it remains relatively rare, the polymorphism could be maintained by negatively frequency-dependent selection (see Futuyma 1986). Or, if male discrimination between morphs is affected either by male-male competition for mates or the rate of encounters with females, the relative mating efficiency of morphs may fluctuate with the operational sex ratio or female density, respectively.

I here define 'mating efficiency' for a mated female as the inverse of the number of times she mates per clutch laid. 'Mating failure' refers to a female's failure to obtain at least one copulation that results in a sufficient load of viable sperm. Multiple matings typically correlate with male fitness, but not with female fitness for species that can use stored sperm to fertilize all of their eggs after a single mating (e.g. Grieve 1937; Fincke 1987, 1988; Cordero 1990b). To the extent that they offer no benefit (but see Fincke 1986a, 1987), multiple matings are disadvantageous to females because they require females to spend more time at the breeding site when they might otherwise be foraging. Other possible fitness 'costs' of multiple matings are damage incurred by males and greater predation pressure at breeding sites than in forag-

ing areas. Heterospecific tandems not only decrease mating efficiency but would represent a substantial loss of fitness if sterile eggs were laid as a result (e.g. Oppenheimer & Waage 1987).

For odonates, an understanding of the maintenance of the polymorphisms in populations and an adequate rejection of the null hypothesis require the following data for each female morph: (1) frequency of multiple matings with different males per visit to the mating site, (2) the frequency of interspecific tandem pairings, (3) life span of marked individuals, (4) frequency and duration of ovipositions, and (5) emergence pattern and rate of sexual maturation. Additionally, some authors have cited male discrimination between morphs (i.e. either pinned or tethered females) as a mechanism that may allow andromorphs to enjoy reduced harassment from either conspecific (e.g. Robertson 1985; Cordero 1989; Córdoba-Aquilar 1992) or heterospecific (De Marchi 1990; Forbes 1991) males.

Past studies on odonates that reported selective benefits and/or costs to either morph have failed to demonstrate statistically significant differences between the morphs in terms of fitness correlates. Johnson (1975) found that the frequency of andromorphic *I. damula* was greater when it was sympatric with *I. demorsa* than when the species were allopatric (9–27% versus 1–5%, respectively). Of 220 *I. damula* males observed in tandem with females, 18 were heteromorphic *I. demorsa*, whereas none were mispaired with andromorphic *I. demorsa*. At the highest observed andromorph frequency (0.27), the lack of heterospecific pairings with andromorphs was significantly less than that expected by chance ($\chi^2=6.7$, $df=1$, $P<0.01$). Nevertheless, at the lower morph frequency (0.09), the expected number of heterospecific tandems with andromorphs was only 1.6, too low to differentiate the expected from the observed value of 0. Thus, because the 220 tandems represented pooled data from several sympatric populations with varying morph frequencies over a 5-year period, it is impossible to test statistically whether andromorphs formed fewer interspecific tandems than expected by chance alone. Similarly, Johnson's method of estimating daily female survivorship for *I. demorsa* (0.90 for heteromorphs and 0.74 for andromorphs) prevented him from showing that differences in survivorship were statistically significant. In order to be accurate, mark-recapture estimates require a high

frequency of recaptures. Even if one conservatively assumes that each of Johnson's recaptures (Table 3 in Johnson 1975) was a unique individual, at best only 32% of the marked heteromorphs and 22% of the andromorphs could have been resighted during the 9-day study period.

In a later study, Robertson (1985) concluded that andromorphic *I. ramburi* were 'male mimics', selectively favoured because, once mated, they enjoyed increased mating efficiency by avoiding harassment from males seeking mates. Robertson's conclusion rested on the finding that the mating frequency of andromorphs (17% of total tandems seen over 24 days) was less than expected from their frequency in the population (30% of a 2-day sample). Robertson's conclusions were valid only if the frequency of receptive andromorphs in his 2-day sample was representative of their frequency in the population over the entire 24-day span, a questionable assumption (see Results). Furthermore, Robertson did not demonstrate any differential cost to heteromorphs or andromorphs. Only four of the heteromorphs were found mating more than once during the 24-day period. Moreover, no females were observed to form more than a single tandem on any given day. These findings are surprising if heteromorphic females were less adept than andromorphs at avoiding unwanted male attention, either on a given day or between oviposition of successive clutches. Moreover, late in the day when females oviposited, both morphs effectively repelled males (H. M. Robertson, personal communication, 1992).

Hinnekin's (1987) conclusion that andromorphic females of *I. elegans* were selected against at low male densities was based on a positive correlation between the frequency of andromorphs and male density of three populations studied by Parr (1969). However, the frequency of andromorphs in Parr's three populations (0.35, 0.33 and 0.27) were not significantly different from each other ($\chi^2=3.0$, $df=2$, $P>0.1$). Furthermore, Hinnekin did not demonstrate any cost to female andromorphs at low male densities.

More recently, Cordero (1992) analysed matings by two types of heteromorphs and an andromorph in two populations of *I. graellsii*, and reported that a greater proportion of andromorphs than heteromorphs failed to mate in a 'low density' population. Although Cordero concluded that his results supported Hinnekin's

density-dependent hypothesis, closer scrutiny reveals that his data failed to reject the null hypothesis. First, the proportion of females that were not seen to mate did not differ significantly among the three morphs ($\chi^2=4.78$, $df=2$, $P>0.05$ rather than $\chi^2=6.76$ as stated in Cordero's Table 7). Second, data on *I. graellsii* did not support Hinnekin's assumption that mating failure of andromorphs results from male discrimination between morphs as potential mates. The total number of observed matings accounted for by each morph (calculated from the mean number of matings $\times N$ in Cordero's Table 7) was random with respect to the frequency of the morph in the sample for both the 'low density' ($\chi^2=3.09$, $df=2$, $P>0.1$) and the 'high density' population ($\chi^2=0.88$, $df=2$, $P>0.5$). Finally, Cordero found no advantage to andromorphs in the 'high density' population that could balance the purported disadvantage to these females in the 'low density' population (see also Fincke, in press). From the above literature critique, I conclude that neither the adaptiveness nor the mechanism maintaining female dimorphism in natural populations has been adequately demonstrated.

Here I report results of an experiment testing males' reactions to tethered females, and demonstrate that male *Enallagma hageni*, like several other coenagrionids, more readily recognize the most abundant morph as 'female'. Nevertheless, male bias towards the majority morph was predictive of neither the timing nor the frequency of tandems by natural females. Results from long-term studies of *E. hageni* and *E. boreale* show that andromorphs and heteromorphs did not differ in any of the fitness correlates measured, consistent with the null hypothesis that colour polymorphism of adult females is selectively neutral in these populations.

METHODS

Experimental Presentation of Individuals to Males

The reaction of males to live tethered females of each morph and control males was noted for *E. hageni* at a large pond near Munro Lake, Cheboygan County, Michigan between 15 and 19 July 1982. Individuals were tethered by gluing a monofilament thread to the thorax with Duco cement. The line was then tied to reed stems, which were placed 0.5 m above the water, 0.5–1.0 m from shore in oviposition areas. So tethered,

the damselflies had too short a lead (1–2 cm) to fly naturally, and they typically remained perched during the trials. Test individuals were captured just prior to the experiment and used for one trial only. Individuals were presented sequentially for timed intervals of 15 min each (three treatments, nine total trials). Male responses to tethered females were divided into five mutually exclusive categories: (1) perching, (2) hovering, (3) grabbing, (4) tandem formation, and (5) attempted take-over of females already in tandem. Removing or marking males that responded would have disrupted the experiment. It is thus possible that the same male made multiple responses during the 15-min period. Nevertheless, because marked males typically flew out of the area after inspecting the test individual, it is unlikely my results were biased by repeated, atypical responses of a few males. The frequency of andromorphs in this population was 0.26, determined by capturing 39 single females on 15 and 16 July.

I compared my results with those from similar past experiments using pinned or tethered individuals. Because methods varied slightly among authors, I designated 'grabbing' or 'tandem formation' as positive sexual responses by males. I report the proportion of total positive sexual responses by males to andromorphs, heteromorphs, and control males (when the latter were included in the experiment).

Mating Frequency and Fitness Correlates of *Enallagma* Morphs

From 12 June to 8 July 1980, I studied a population of *E. boreale* at a small pond (90-m perimeter) in Munroe County, Michigan (hereafter, 'Barley Pond'). Here, *E. boreale* was the only *Enallagma* present except during the final week when *E. ebrium* began breeding at the pond. Although I observed few mature *E. boreale* before 12 June, I curtailed the study before the breeding season ended in mid-July. On 15 days (overcast days of inactivity were excluded) starting between 0830 and 1300 hours and ending between 1550 and 1830 hours ($\bar{X} \pm \text{SE}$ h of observation/day = 6.8 ± 0.3 h, range = 4.7–8.3 h), I marked the males and females with mature adult coloration that I found around the pond by writing a number in indelible ink on the wing. Over the 23-day span, I measured the forewing and abdomen length of a subset of these males and females. I noted resight-

ings of marked individuals but did not recapture damselflies after the initial marking. I measured relative life span as the time between first and last sightings at the pond. Females with mature coloration when marked were assumed to be sexually receptive because nearly all that were seen at the pond were in tandem. Single adults were common in an adjacent field. I measured the operational sex ratio at the pond as the number of marked males per female sighted. Because I never resighted 78.5% of the 554 females marked, and my study pond was within 0.4 km of another pond on which *E. boreale* bred, for this species only, I limited all but the daily analyses to individuals seen at least once after they were marked, either on the same day or on subsequent days. I stopped marking individuals on 4 July but continued to search the pond areas for females until 8 July to lessen any effect on average life span caused by females marked towards the end of the study. The capture and marking of tandem pairs resulted in their separation. I recorded all multiple tandems by a given female with different males during the same day, and noted tandem females that successfully rejected males. Rejection behaviour included females failing to raise their abdomens to copula position while holding onto a perch, or resisting flight, resulting in a zigzag flight pattern (see Bick & Hornuff 1966). Males usually released such females within a few minutes.

On 18 days between 9 July and 3 August 1980, I measured survivorship and mating frequency of *E. hageni* at an isolated pond ('East Point Pond', 110-m perimeter) at the University of Michigan Biological Station near Pellston, Michigan. At this site *E. hageni* was the only *Enallagma* present during the study (although a few *E. carunculatum* were found at the pond in mid-August). Beginning between 0830 and 1300 hours, and ending between 1600 and 1830 hours ($\bar{X} \pm \text{SE}$ h of observation/day = 6.1 ± 0.4 h, range = 4.1–8.2 h), I marked individuals and noted the presence of marked individuals and tandem pairs. On day 8 of this study, a storm developed around noon before many females arrived at the pond. Consequently the operational sex ratio was abnormally large (9.8), nearly twice that of the second largest ratio. I thus excluded day 8 from the correlations between daily mating efficiency of *E. hageni* morphs and the operational sex ratio, density, and morph frequency. Otherwise, methods were similar to those above and are described in detail

Table I. Number of male responses to live tethered female *E. hageni* during 15-min trials (three per test group)

Test individual	Perch	Hover	Grab	Tandem	Attempted take-over
Heteromorph	12 (15.2)	56 (101.2)	118 (84.2)	21 (10.1)	13 (7.4)
Andromorph	14 (12.5)	101 (83.6)	62 (69.5)	1 (8.4)	3 (6.1)
Male	7 (5.0)	63 (33.0)	3 (27.5)	0 (3.3)	0 (2.4)

Numbers in parentheses are the expected values if the type of response to the test individuals was random ($\chi^2=116.7$, $df=8$, $P<0.025$).

elsewhere (Fincke 1982). For both species in 1980, all data refer to individuals marked as sexually mature adults. For both species, I analysed the data by seasonal period (i.e. days 1–10, 11–19, and 20–25) to detect possible trends in fitness correlates among females that became sexually mature in early, mid- and late season. In 1980, the number of marked individuals seen daily was a good estimate of male and female density at the breeding site because in this year both study species were marked and resighted only within 7 m of the pond perimeter. Throughout, means are presented with standard errors, and *t*-tests are two-tailed.

In 1982, from 26 June to 29 July, I marked and resighted *E. hageni* around East Point Pond and in an adjacent field where females and males could be found on days when they were not at the pond. In this year I concentrated on measuring total oviposition duration of a subset of females that were followed as tandem pairs until the female finished ovipositing that day. Oviposition completion was determined either when a female, upon resurfacing, successfully resisted a male's tandem attempt, or flew away from the pond and was not seen again that day (see Fincke 1986a for details). For females that visited the pond more than once, I calculated the inter-clutch interval as the number of days between visits to the pond (i.e. minimum interval was 1 day for a female returning the next day).

At East Point Pond, from 7 June to 5 July 1981, I marked newly emerged *E. hageni* on the thorax with a dab of enamel (colour-coded to day), whereas I wrote numbers on the hardened wings of teneral that were a day old or older (indicated by wing condition). I also marked sexually mature individuals (indicated by body coloration) at the

pond and in the adjacent field daily until 15 July. As mature individuals started arriving at the pond around 16 June, I concentrated on recording matings and adults at the pond. In contrast with the other study years, in 1981 the population of *E. hageni* emerged early and declined early and abruptly, with fewer than five tandem pairs seen daily from 10 to 12 July. For *E. hageni*, the study period in all years spanned 80–100% of the breeding season and, in 1981, some unknown portion of the emergence period.

RESULTS

Male Responses to Experimental Individuals

Because the reaction of *E. hageni* males to the three treatment groups was similar across the three trials, results were pooled (Table I). Males responded in a sexual manner (i.e. grabbed females, formed tandems, or attempted take-over of a female already in tandem) more frequently to heteromorphs than they did to andromorphs ($\chi^2=51.4$, $df=4$, $P<0.005$). Nevertheless, males responded sexually to andromorphs more frequently than they did to control males ($\chi^2=27.7$, $df=4$, $P<0.005$).

Table II presents comparative data on the proportion of total sexual responses that males showed to individuals of each treatment group, and the reported frequency of andromorphs in the study populations. For seven of the nine species listed, males responded sexually more frequently to the most abundant morph in the population. Moreover, among coenagrionids, the proportion of the total sexual response to females that was directed towards andromorphs was correlated

Table II. Comparison of the proportion of total sexual responses (grabbing or tandems) by males to pinned or tethered individuals and the frequency of andromorphs in the populations

Species	Sexual response to			Andromorph frequency	Source
	A	H	Male		
Coenagrionidae					
<i>Enallagma</i>					
<i>boreale</i>	0.67	0.33	—	0.68	Forbes (in press)
<i>ebrium</i> *	0.16	0.84	—	0.05	Forbes 1991
<i>hageni</i>	0.30	0.69	0.01	0.26	Fincke this paper
<i>Ischnura</i>					
<i>ramburi</i>	0.34	0.47	0.19	0.31	Robertson 1985
<i>graellsii</i>	0.18	0.67	0.14	0.14	Cordero 1989, 1990b
<i>denticollis</i> †	0.35	0.65	0.00	—	Córdoba-Aguilar 1992
<i>Argia</i>					
<i>apicalis</i>	0.35	0.65	—	0.48	Bick & Bick 1965
<i>vivida</i>	0.42	0.58	—	0.66	Table 1 in Conrad & Pritchard 1989
Calopterygidae					
<i>Calopteryx</i>					
<i>splendens</i>	0.52	0.48	—	0.10	De Marchi 1990

A: Andromorphs; H: heteromorphs.

*Response to *E. boreale* females, whereas the frequency of andromorphs is that for *E. ebrium*.

†Andromorphs represented the minority of mated females, but the frequency of andromorphs in the population at large was not provided.

positively with the frequency of andromorphs in the population ($r=0.86$, $N=7$, $P<0.05$). In the case of *E. ebrium* (Forbes 1991), males were presented with morphs of *E. boreale*, which are similar in colour to those of *E. ebrium*. *Enallagma ebrium* males responded to *E. boreale* females as if they were conspecifics, showing a preference for heteromorphs, the majority morph in the *E. ebrium* population, but the minority morph in the *E. boreale* population. In *Argia vivida*, the reaction of males to the two morphs did not differ from 1:1 (Conrad & Pritchard 1989) although andromorphs were more abundant than heteromorphs. *Calopteryx splendens* males also did not display a preference for either morph despite the low frequency of andromorphs in the study population. However, unlike the coenagrionids tested, andromorphic *C. splendens* differed from heteromorphs in wing, rather than body, colour.

Morph and Mating Frequency

For both *E. hageni* and *E. boreale*, the thorax and abdomen of heteromorphs were dull or

brownish green, whereas those of andromorphs were blue, similar to, but not as bright as, male coloration. For both species, none of the females marked as mature adults in any year were found to change from one morph to the other although one marked *E. boreale* was of intermediate colour. Of the total 554 mature *E. boreale* females marked over the 23-day study in 1980, 45% were andromorphs, significantly higher than the frequency of andromorphic *E. hageni* at East Point Pond in the same year ($\chi^2=26.6$, $df=1$, $P<0.005$). Over the 3-year span, the frequency of sexually mature andromorphic *E. hageni* at East Point Pond did not vary significantly: 26% in 1980 ($N=370$), 31% in 1981 ($N=166$) and 36% in 1982 ($N=103$, $\chi^2=4.3$, $df=2$, $P>0.1$).

My estimate of the effective population size (see Futuyma 1986) of *E. boreale* was 949 (4×431 marked, mated males \times 528 mated females/959). For *E. hageni*, the effective population size varied from 695 in 1980 (338 mated males and 358 females) to 181 in 1981 (87 mated males and 94 females). I saw 114 males and 90 females mating in 1982, but this sample underestimated the

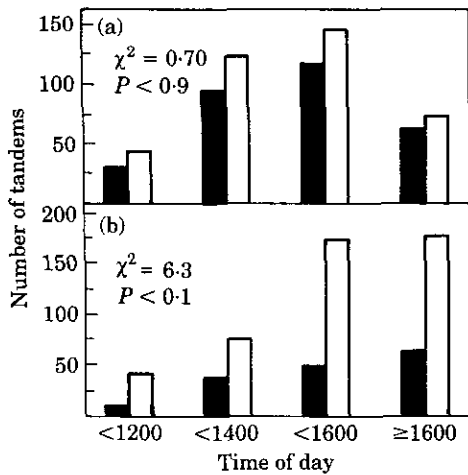


Figure 1. Time of day tandems were first sighted (1980 data) for andromorphic (■) and heteromorphic (□) female *E. boreale* (a) and *E. hageni* (b).

effective population size because my observations were concentrated on only a subset of marked individuals.

The mating and oviposition behaviour of *E. boreale* was similar to that of *E. hageni* which has been described elsewhere (Fincke 1982, 1988). For both species, females came to the breeding site only after they had mature eggs and were receptive to mating. Mating duration of *E. boreale* was about a half hour ($\bar{X}=25.5 \pm 2.5$ min, $N=2$), similar to that of *E. hageni* (Fincke 1982). After mating, a male remained in tandem with his mate until she climbed headfirst down an emergent plant stem, where she oviposited under water. Females remained under water for as long as 80 min, and upon resurfacing were either taken in tandem by guarding mates or other males, or flew away from the pond. Five and four andromorphs versus seven and 13 heteromorphs of *E. boreale* and *E. hageni* (1982 data), respectively, were seen to reject males that had taken them in tandem after resurfacing. For neither species was there a significant difference in the time of day females of each morph were first observed in tandem (Fig. 1). Furthermore marked males that mated more than once did so randomly with respect to female colour morph (Table III).

The frequency of daily and lifetime tandems were random with respect to morph colour. None of the 23 and 21 daily mating frequencies by andromorphic and heteromorphic female

E. boreale and *E. hageni* respectively listed in Tables IV and V differed from that expected if mating frequency reflected only the number of each morph present at the pond (χ^2 tests). Over the study, andromorphs accounted for 305 (0.44) of the total 686 *E. boreale* tandems observed ($\chi^2=0.26$, $df=1$, $P>0.5$), and for 161 (0.26) of the 630 *E. hageni* tandems observed ($\chi^2=2.0$, $df=1$, $P>0.1$).

Reproduction and Survivorship of Morphs

In 1980, for both *E. boreale* and *E. hageni*, there was no difference between heteromorphs and andromorphs in size, life span, number of visits to the pond (a function of the number of clutches matured and, in this year, the number of days a female was seen), the number of mates per clutch, or total tandems per life span (Table VI). In addition, andromorphic *E. hageni* did not differ from heteromorphs in oviposition duration, inter-clutch interval, or maturation rate (Table VII). In 1982, 19% of the 37 sexually mature *E. hageni* andromorphs and 14% of the 66 heteromorphs were not seen to mate, no different from that expected if mating failure was random with respect to female colour ($\chi^2=0.50$, $df=1$, $P>0.5$). All but four of the unmated females were sighted only once, whereas mated females were sighted repeatedly.

In 1980, the mean density of male *E. hageni* (excluding days with less than 10 mature males at the pond) was about three times higher ($\bar{X}=95.9 \pm 11.5$ males, range=16–167, $N=15$ days), than it was in 1981 ($\bar{X}=30.7 \pm 3.9$ males, range=10–64, $t=5.3$, $N=21$ days, $P<0.001$) when the population declined abruptly. Nevertheless, in 1981, there was no difference between the morphs in the number of matings obtained or in their mating efficiency (inverse of 'mates/clutch', Table VI). As shown in Table VIII, 55% of the mature andromorphs and 37% of the heteromorphs were not seen to mate. For females seen once (70% of total), there was no difference in mating failure between morphs, whereas andromorphs seen 2 or more days were less likely than heteromorphs to be seen mating. However, these females were also sighted relatively less often and over a shorter time span. Thus, the relatively greater mating failure of andromorphs in this year did not result from discrimination between morphs by mating males. Despite the longer life span of

Table III. Distribution of matings with respect to colour morphs by individual males (*N*) mating at least twice in their life (1980 data)

		Distribution of matings					χ^2
<i>N</i>							
Two matings		AA		AH		HH	
<i>E. boreale</i>	76	21 (15.39)		34 (37.63)		21 (22.99)	2.56 NS
<i>E. hageni</i>	87	5 (6.82)		30 (35.08)		52 (45.10)	2.28 NS
Three matings		AAA	AAH	AHH		HHH	
<i>E. boreale</i>	24	1 (2.18)	6 (7.99)	16 (9.79)		1 (3.99)	7.85 NS
<i>E. hageni</i>	43	0 (0.94)	6 (7.28)	18 (18.72)		19 (16.04)	1.70 NS
Four matings		AAAA	AAAH	AAHH	AHHH	HHHH	
<i>E. boreale</i>	7	0 (0.29)	0 (1.4)	5 (2.57)	2 (2.10)	0 (0.64)	4.63 NS
<i>E. hageni</i>	10	0 (0.63)	2 (0.63)	2 (2.44)	2 (2.44)	4 (4.18)	5.45 NS

A: Andromorphs; H: heteromorphs.

Only two male *E. hageni* mated more than four times, whereas no *E. boreale* males did so. Expected values in parentheses were calculated using the mean frequency of morphs in the two populations.

Table IV. Number of *E. boreale* female morphs found daily in tandem, alone, and in multiple sequential tandems with different males, and the total number of unique males and females present at Barley Pond

Day	% Total	Andromorphs			Heteromorphs			Males/females
		Tandem	Solo	Multiple matings	Tandem	Solo	Multiple matings	
1	63%	5	0	0	3	0	0	23/8
2	47%	8	0	0	9	0	0	45/17
5	74%	17	0	0	7	0	1	64/23
6	63%	15	1	1	9	0	0	115/24
9	45%	28	0	4	30	1	2	94/53
10	46%	21	0	2	23	2	3	115/41
11	31%	11	0	3	24	1	7	129/26
12	44%	27	2	6	35	0	6	108/52
13	49%	54	2	7	58	0	6	152/101
14	46%	23	1	3	27	0	2	180/46
15	33%	24	1	1	54	2	7	143/73
19	39%	14	1	1	23	1	2	140/36
21	38%	16	1	4	18	7	4	109/34
22	36%	13	1	0	30	0	5	109/39
23	45%	29	0	8	31	0	5	128/47

The total number of individual females present=tandem+ solo - multiple matings.

heteromorphs in this year, as a result of long inter-clutch intervals, heteromorphs did not visit the breeding site more often than andromorphs (Table VI).

Table IX shows the morph frequency of tenerals, the proportion of teneral *E. hageni* surviving to sexual maturity, and the frequency of individu-

als marked as mature adults in 1981 and 1982. About a third of the teneral females could not be identified to morph because they were too pale at the time of marking and they were not resighted. Of the tenerals scored as andromorphs that were later found as adults in 1981, two (4%) were resighted as mature heteromorphs, indicating that

Table V. Number of *E. hageni* female morphs found daily in tandem, alone, and in multiple sequential matings with different males, and the total number of unique males and females present at East Point Pond (1980 data)

Day	% Total	Andromorphs			Heteromorphs			Males/females
		Tandem	Solo	Multiple matings	Tandem	Solo	Multiple matings	
1	23%	5	1	1	16	3	2	122/22
2	26%	21	0	4	59	2	12	156/66
3	22%	32	1	11	93	0	15	147/100
4	23%	16	0	5	46	1	11	90/47
5	37%	13	0	2	24	0	5	167/30
7	28%	19	0	3	45	2	5	121/58
8	46%	5	1	0	8	0	1	128/13
9	19%	12	0	4	47	2	15	84/42
10	38%	1	4	0	4	4	0	55/13
14	33%	8	3	2	18	5	5	100/27
15	24%	11	3	2	47	3	11	92/51
16	18%	5	1	0	33	2	8	72/33
19	22%	4	1	1	11	5	2	52/18
20	30%	7	0	1	14	3	3	36/20
21	33%	2	1	1	4	1	1	16/6

The total number of individual females present = tandem + solo - multiple matings.

the frequency of teneral andromorphs was less than or equal to 58.6%. Comparison of the proportion of tenerals marked that were later resighted as mature adults indicated that survivorship to sexual maturity did not differ between the morphs ($\chi^2=1.37$, $df=1$, $P>0.1$). Nevertheless, although andromorphs represented 59% of the sample of females marked as tenerals, they represented only 24% of the females marked as adults. These seemingly contradictory results are parsimoniously explained if relatively more heteromorphs than andromorphs emerged before I began marking tenerals on 7 June. This sampling bias would result in a shorter life span of mature andromorphs, because they would have been younger at the time of the population decline. Of the 166 mature females for which life span data are presented, 39% of the andromorphs and 16% of the heteromorphs were marked as tenerals.

Similarly, in 1982, there was no difference between morphs in the proportion marked as tenerals that were resighted as sexually mature females ($\chi^2=1.83$, $df=1$, $P>0.1$). Nevertheless, andromorphs represented 48% of the teneral females but only 37% of the females marked as adults ($\chi^2=4.5$, $df=1$, $P<0.05$). In this year, of the 103 sexually mature females for which data

on life span were available, 14% of the andromorphs and 17% of the heteromorphs were marked as tenerals.

Predation on adults and teneral damselflies at the two study sites is shown in Table X. Additionally, over the course of the study six *E. boreale* females were found dead in the water or on aquatic vegetation, suggesting that submerged oviposition carries a risk of mortality in this species as it does for *E. hageni* (Fincke 1986a). Five *E. boreale* females found in tandem were missing all or parts of wings, and one was missing her abdomen. Such damage seemed to be caused by the large number of males that harassed tandem pairs at the oviposition sites.

Daily and Seasonal Effects of Sex Ratio, Density, and Morph Frequency on Mating Efficiency of Morphs

In 1980, the mean daily operational sex ratio for *E. boreale* was 2.9:1 (males:females, range=1.5-4.9), and 2.9:1 for *E. hageni* (range=1.4-5.6). For both species, there was a positive correlation between the number of females at the pond and the number of males present (Fig. 2). The number of females present was correlated negatively with the operational sex ratio in *E. boreale* ($r = -0.58$,

Table VI. Mean fitness correlates and mating frequency of andromorphic and heteromorphic females

		Andromorph	Heteromorph	<i>t</i> †
Wing length (mm)				
<i>E. boreale</i>	1980	19.96 ± 0.2 (<i>N</i> =25)	19.53 ± 0.2 (<i>N</i> =19)	-2.19 NS
<i>E. hageni</i>	1980	18.26 ± 0.1 (<i>N</i> =77)	18.21 ± 0.04 (<i>N</i> =228)	0.46 NS
Life span (days)				
<i>E. boreale</i>	1980	3.60 ± 0.54	3.31 ± 0.37	0.44 NS
<i>E. hageni</i>	1980	2.21 ± 0.26	2.19 ± 0.18	0.04 NS
	1981	1.7 ± 0.22	2.5 ± 0.29	-2.22*
	1982	7.32 ± 1.06	8.04 ± 1.08	-0.48 NS
Visits to pond				
<i>E. boreale</i>	1980	1.36 ± 0.08	1.44 ± 0.08	-0.71 NS
<i>E. hageni</i>	1980	1.36 ± 0.06	1.31 ± 0.04	0.69 NS
	1981	1.09 ± 0.60	1.21 ± 0.65	-1.37 NS
	1982	1.43 ± 1.01	1.92 ± 1.60	-1.91 NS
Mates/clutch				
<i>E. boreale</i>	1980	1.67 ± 0.08 (<i>N</i> =53)	1.69 ± 0.08 (<i>N</i> =65)	-0.14 NS
<i>E. hageni</i>	1981	1.25 ± 0.13 (<i>N</i> =23)	1.09 ± 0.03 (<i>N</i> =72)	1.15 NS
	1982	1.24 ± 0.07 (<i>N</i> =30)	1.15 ± 0.05 (<i>N</i> =57)	1.07 NS
Tandems with unique males				
<i>E. boreale</i>	1980	2.09 ± 0.10	2.21 ± 0.10	-0.80 NS
<i>E. hageni</i>	1980	1.56 ± 0.10	1.52 ± 0.06	0.34 NS
	1981	0.61 ± 0.11	0.83 ± 0.08	-1.56 NS
	1982	1.73 ± 0.20	2.17 ± 0.22	-1.44 NS

A: Andromorphs; H: heteromorphs.

Unless noted otherwise, sample sizes are *E. boreale* 53A, 66H; *E. hageni* 1980: 96A, 274H; 1981: 51A, 115H; 1982: 37A, 66H. Difference in life span of *E. hageni* between 1980 and 1982 was an artefact of sampling (see Methods).

**P*<0.05.

†Student's *t*-test.

N=15, *P*<0.02) but not in *E. hageni* (*r*=-0.49, *N*=14, *P*>0.05). Daily operational sex ratio was not correlated with the density of males at the breeding site for either *E. boreale* (*r*=0.17, *N*=15 days, *P*>0.5) or *E. hageni* (*r*=0.25, *N*=14 days, *P*>0.3). As shown in Table XI, for both species, the daily mating efficiency of females of either morph was not correlated with the operational sex ratio, or with the density of males or females. For *E. boreale* but not for *E. hageni*, mating efficiency of heteromorphs was correlated positively with the frequency of andromorphs. The correlation for andromorphs, although not significant, was also positive.

For *E. boreale*, there was a seasonal decline in the number of andromorphs seen for the first time at the pond (*r*=-0.64, *P*<0.01). As shown

in Fig. 3a, this decline paralleled the decline in frequency of andromorphs visiting the pond daily. Because the number of *E. boreale* males present at the pond increased over the same time span, the frequency of andromorphs at the pond was correlated negatively with the density of males (*r*=-0.52, *P*<0.05), but was not correlated with the operational sex ratio (*r*=-0.01, *P*>0.9). For *E. hageni*, the density of both males and females decreased significantly over the study but the frequency of andromorphs at the pond was not correlated with either the day of study (Fig. 3b), the density of males (*r*=-0.08, *P*>0.7), or the operational sex ratio (*r*=0.50, *P*>0.07). Despite seasonal trends in male density at the pond for both species, and in the frequency of andromorphic *E. boreale*, there were

Table VII. Lifetime fitness correlates of andromorphic and heteromorphic *E. hageni* females

	Andromorphs		Heteromorphs		<i>t</i> *
	<i>N</i>	$\bar{X} \pm SE$	<i>N</i>	$\bar{X} \pm SE$	
Oviposition (min)/life span	19	42.7 ± 5.7	35	45.9 ± 6.1	-0.33 NS
Oviposition (min)/clutch	19	29.7 ± 3.5	35	28.5 ± 2.9	0.25 NS
Inter-clutch interval (days)	11	7.9 ± 1.6	30	6.2 ± 0.7	1.09 NS
Maturation rate (days)	17	8.4 ± 1.2	14	7.6 ± 1.2	0.49 NS

All data are from 1982 except for maturation rate (1981).

*Student's *t*-test.

Table VIII. Mating failure of *E. hageni* morphs in 1981

	Andromorphs	Heteromorphs	χ^2	<i>P</i>
Females seen once				
Mated	16 (18.18)	41 (38.82)	0.75	>0.1
Unmated	21 (18.81)	38 (40.18)		
Females seen ≥ 2 days*				
Mated	7 (10.64)	31 (27.36)	7.2	<0.01
Unmated	7 (3.36)	5 (8.64)		

Expected values in parentheses were calculated from the proportion of the morphs in the samples.

*In this class, andromorphs were sighted less often ($\bar{X}=2.1 \pm 0.07$ days) than heteromorphs ($\bar{X}=2.5 \pm 0.11$ days, $t=-3.08$, $P<0.01$) and had shorter life spans ($\bar{X}=3.5 \pm 0.55$ days) than heteromorphs ($\bar{X}=5.8 \pm 0.65$ days, $t=-2.63$, $P<0.05$).

no seasonal effects on fitness correlates with respect to morph type (Table XII). Although female life span in *E. hageni* declined in late season, this decline did not differ between colour morphs.

DISCUSSION

Male Bias Towards the Majority Morph

Results of my experiment with tethered individuals coupled with those of past experiments with pinned or tethered females suggest that coenagrionid males more readily recognize as 'female' the most abundant morph in a given population. A frequency-dependent mode of male discrimination, reminiscent of search image formation by foraging vertebrates (e.g. Mook et

al. 1960; Tinbergen 1960; Paulson 1973), more parsimoniously explains the comparative data in Table II than does the 'male mimicry' mechanism proposed by Robertson (1985). Because the daily frequency of morphs at the pond varied considerably, plasticity in search image formation would seem to be more advantageous than a fixed one for a given male or population. For both *E. boreale* and *E. hageni*, a male's search image was not fixed with respect to male genotype (see also Conrad & Pritchard 1989; Cordero 1992), in contrast with Johnson's (1975) finding that *I. damula* males were either 'androphilic' or 'heterophilic' when provided with a surplus of females under laboratory conditions. Plasticity of search image formation by males within a population is currently being investigated experimentally.

Table IX. Number of *E. hageni* marked as teneral and adults in 1981 and 1982 at East Point Pond

Year	Tenerals marked				Tenerals resighted as mature adults			Adults marked		
	A	H	U	Males	A	H	Males	A	H	Males
1981	73	48	53	145	20	18	58	31	97	230
1982	13	14	11	32	5	11	22	32	55	142

A: Andromorphs; H: heteromorphs; U: female morph colour undetermined.

Table X. Number of observed acts of predation on tandem pairs, single adults and tenerals of *E. hageni* and *E. boreale* (1980, 1981)

	Tandem pairs	Single adults		Tenerals	
		Males	Females	Males	Females
Spiders (orb weavers)		20	1	2	1
Ground spiders	1*				
Water scorpions	1		3		
Robber flies		2	1		
Grasshoppers	1*	1	1		
Diving beetles			1		
Gomphid dragonflies	1	3	1		
Frogs	1*	3	1		
<i>I. verticalis</i> damselfly females				3	1

*Indicates only the tandem female was known to be eaten.

In contrast with my conclusion that males more readily recognize the majority morph as 'female', De Marchi (1990) found that male *Calopteryx splendens* responded equally to live, tethered andromorphs and heteromorphs, despite the fact that andromorphs represented only 10–13% of the females in the population. Unlike coenagrionids listed in Table II, whose males search for females, *C. splendens* males defend oviposition sites that attract females, thereby decreasing the value to males of a search image for conspecific females. However, because heterospecific *Calopteryx* also used the same oviposition sites, the ability of males to discriminate between conspecific and heterospecific females would be adaptive. On the other hand, if males primarily recognize the sex of conspecifics by flight patterns, but in the absence of such cues determine sex by wing coloration, this latter ability could not have been detected without preventing females from flying (De Marchi used a long tether which enabled females to fly around naturally).

Unlike vertebrate search images which result in frequency-dependent shifts in the prey taken (e.g. Holling 1959; Greenwood & Elton 1979; Pietrewicz & Kamil 1981), the bias of male *E. hageni* for tethered females of the majority morph did not result in these females being taken in tandem sooner in the day or more frequently. This was not surprising, given that loss of a potential mate has greater fitness consequences for a male damselfly than loss of a potential prey item has for a bird. For both *Enallagma* species, only about a third of the mature males were seen to mate over their lifetime, suggesting strong selection on male mate-finding ability. In fact, male *E. hageni* reacted significantly more positively to tethered andromorphs than they did to tethered conspecific males, indicating that males were able to distinguish andromorphs from male conspecifics (see also Bick & Bick 1965; Robertson 1985; Córdoba-Aguilar 1992). The finding that males discriminate between morphs, coupled with the

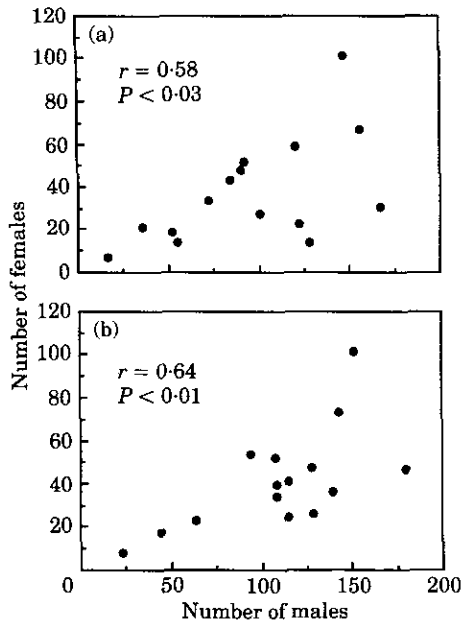


Figure 2. The number of *E. boreale* (a) and *E. hageni* (b) females present as a function of the number of males at the pond (1980 data).

lack of differences between morphs in mating frequencies under natural conditions, suggest that andromorphs and heteromorphs use different behaviour patterns to avoid detection by males (e.g. Robertson 1985; Cordero 1989; Córdoba-Aguilar 1992), but that they do so with equal success.

Failure to Reject the Null Hypothesis

Mating and reproductive success

My study failed to uncover any advantage to andromorphic females of 'mimicking males'. After ovipositing, heteromorphs were as likely as andromorphs to resist additional matings by males taking them in tandem. Moreover, my analysis of daily matings cast some doubt on Robertson's (1985) conclusion that *I. ramburi* andromorphs mated less frequently relative to their abundance than did heteromorphs. Had I compared, as did Robertson, the proportion of total tandems by andromorphs with the frequency of andromorphs at the pond on any 2 days of the study, I could have concluded that *E. boreale* andromorphs mated either more (e.g. days 5 and

6, Table IV) or less frequently than expected by chance (e.g. days 15 and 19), when in fact males mated randomly with respect to the daily frequency of available morphs (see also Conrad & Pritchard 1989; Cordero 1992). Female *E. hageni* morphs did not differ in oviposition duration, inter-clutch interval, or rate of sexual maturation. Similarly, Thompson (1989) found no difference between the two morphs of *Coenagrion puella* in the rate of sexual maturation or the number of clutches laid.

Alternatively, differences between the biology of *Ischnura* and other coenagrionids may account for a selective advantage to andromorphs in *I. ramburi* but not in other species. Whereas unreceptive female *E. boreale* and *E. hageni* avoid the breeding site during days between maturation of egg clutches, *I. ramburi* females continue to feed and rest around the breeding site (H. M. Robertson, personal communication, 1992) where they may be harassed by males. Furthermore, multiple matings may represent a greater relative 'cost' for *I. ramburi* because they mate for as long as 3 h and do not submerge to oviposit. In contrast, *E. boreale* and *E. hageni* mate for about half an hour and females exchange matings for male guarding which decreases the chances that a female drowns after oviposition. Interestingly, I saw only one andromorph in an *I. verticalis* population ($N=533$ females) where females effectively rejected multiple matings by using wing displays and were essentially monogamous (Fincke 1987). Nevertheless, in *I. graellsii*, which has copulations as long as those in *I. ramburi*, mating frequency did not differ between andromorphs and heteromorphs (Cordero 1992).

Contrary to Hinnekint's (1987) hypothesis that andromorphs should be favoured at high male densities but not at low male densities, I found no density-dependent mating benefits or costs for morphs of either *Enallagma* species in spite of a seven-fold fluctuation in the daily density of males and a seasonal effect on male density around the ponds. The frequency of *E. boreale* andromorphs visiting the pond actually decreased as male density increased. Because the operational sex ratio, which was always male biased, was not correlated with male density, I conclude that the negative correlations between the number of females and the operational sex ratio were a consequence, rather than the cause, of low female density on certain days. Hinnekint (1987) used a similar

Table XI. Correlations between the mean daily mating efficiency of female morphs, and the operational sex ratio, density of males and females, and andromorph frequency of *Enallagma* study species in 1980

	Operational sex ratio	Male density	Female density		Andromorph frequency
			A	H	
<i>E. boreale</i>					
Andromorph	-0.14	-0.44	-0.17	-0.26	0.44
Heteromorph	-0.11	-0.35	-0.03	-0.26	0.53*
<i>E. hageni</i>					
Andromorph	0.25	0.11	-0.05	-0.14	0.11
Heteromorph	0.35	-0.08	0.06	-0.05	0.36

A: Andromorphs; H: heteromorphs.

Mating efficiency = 1/mates/clutch.

E. boreale, $N=15$ days; *E. hageni*, $N=14$ days.

* $P<0.05$.

negative correlation to conclude that females were repelled from the breeding site at high male densities. However, because males visit the pond more often than do females (Fincke 1982), a high operational sex ratio could result from chance alone, if relatively fewer females were ready to lay eggs on some days than on others. Moreover, for classes of *E. hageni* females sighted an equal number of days, the proportion of females that were not seen to mate did not differ between morphs, even in 1981 when male density was abnormally low.

Finally, my data did not provide evidence for either frequency-dependent or sex ratio-dependent differences in mating efficiency between the morphs, in spite of as much as a two-fold difference in daily morph frequency at the pond (see also Garrison 1978) and a four-fold difference in daily sex ratio. Furthermore, despite a seasonal effect on male density for both species, and on the frequency of *E. boreale* morphs, mating frequency of the morphs did not fluctuate seasonally in either species. For *E. boreale*, the correlations between mean daily mating efficiency and andromorph frequency (Table XI) coupled with the seasonal trend in male density and andromorph frequency (Fig. 3a), suggested that at even higher male densities, mating efficiency of both morphs would decrease.

Given that my study populations did not overlap with sympatric *Enallagma* species to any great degree, it seems unlikely that andromorphs in this study enjoyed greater reproductive isolation than heteromorphs. Nevertheless, elsewhere in the county, *E. hageni* and *E. ebrium* bred simul-

taneously at the same site. At Barley Pond, *E. boreale* overlapped with *E. ebrium* only late in the season. Females of these two species are very similar, and any interspecific tandems were likely to have been overlooked. However, despite the possibility of interspecific pairings, the specificity of the male abdominal claspers in many coenagrionids that are similar in appearance make it difficult for males to achieve heterospecific tandems (Paulson 1974).

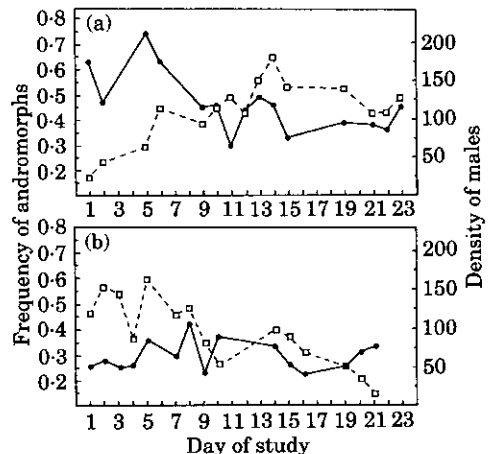


Figure 3. Occurrence of andromorphs (●) and males (□) at the pond. (a) *E. boreale*. Andromorph frequency decreased over the season ($r=-0.64$, $N=15$, $P<0.01$), whereas the density of males increased ($r=0.64$, $N=15$, $P<0.01$). (b) *E. hageni*. Andromorph frequency did not decrease over the season ($r=0.04$, $N=15$, $P>0.7$) although male density did ($r=-0.83$, $N=15$, $P<0.0001$).

Table XII. *F*-values for season and morph effects on female reproduction and fitness in *E. boreale* (1980) and *E. hageni* (1982)

Variable	Treatment effect		
	Season	Morph	Season-morph interaction
Total tandems			
<i>E. boreale</i>	1.25	0.73	0.37
<i>E. hageni</i>	1.02	3.18	1.70
Visits to pond			
<i>E. boreale</i>	1.55	0.90	0.44
<i>E. hageni</i>	1.01	2.44	0.76
Life span (days)			
<i>E. boreale</i>	5.24	0.00	0.59
<i>E. hageni</i>	3.31*	0.03	0.54
Oviposition duration (min)			
<i>E. hageni</i>	1.03	0.10	0.02
Inter-clutch interval (days)			
<i>E. hageni</i>	0.96	0.11	1.89

* $P < 0.05$. ANOVAS were done using GLM procedure of SAS (1988).

Survivorship

Contrary to both the male mimicry (Robertson 1985) and the reproductive isolation hypotheses (Johnson 1975), sexually mature andromorphs in the 1980 and 1982 populations did not suffer higher mortality than the heteromorphs (see also Thompson 1989; Cordero 1992). Similarly, Forbes (1994) found that dragonfly predation on female *E. boreale* was random with respect to colour morph. The common predators in my study populations (Table X) were more likely to detect prey on the basis of their movement rather than on body colour. If predators were more likely to notice the blue andromorph, which in many coenagrionids is less conspicuous to a human observer than is the blue male (Walker 1953), one would expect bright blue males to suffer higher mortality than the drabber females. Yet lifetime survivorship of females (of either morph) and males did not differ in the 1982 *E. hageni* population (Fincke 1986b), or in a population of *I. gemina* (Hafernik & Garrison 1986, andromorphs were lacking in this population).

For *E. hageni*, both the greater proportion of andromorphs in the teneral, relative to the mature, female population in 1981 and 1982, and the shorter life span of mature andromorphs in 1981, were consistent with the hypotheses that survivorship of tenerals and mature females

did not differ between morphs, and that emergence of heteromorphs was earlier than that of andromorphs. Differential emergence of morphs coupled with a sampling bias of tenerals might explain Thompson's finding (1989) that in *Coenagrion puella*, andromorphs accounted for 5.4% of the tenerals marked but represented 11.8% (not 13.3% as stated in the text) of those surviving to sexual maturity, despite no differences between morphs in survivorship of mature females. The reason for morph differences in the timing of emergence is unclear. None the less, in *E. boreale*, sexually mature andromorphs appeared in the population earlier in the season than did heteromorphs. If genes for body colour and for the timing of emergence were in linkage disequilibrium (see Futuyma 1986), colour polymorphism in females might be an incidental effect of fluctuating selection on emergence.

Stability of morph frequencies

By itself, the stability of morph frequencies that I found in the *E. hageni* population over a 3-year period is consistent with both the null and the adaptive hypotheses. The null hypothesis predicts no change in morph frequencies from year to year in the absence of drift, mutation, selection and/or migration (i.e. Hardy-Weinberg equilibrium, see Futuyma 1986). Even given the low population

density of *E. hageni* in 1981, the effective population size in that year was at least 181, too large for drift to have significant consequences on morph frequencies during the study period. The adaptive hypotheses also predict no change in morph frequency, given that the population is at equilibrium and the selective pressures on each morph are similar from year to year. However, despite an abnormally low density of males in 1981, a decline in andromorph frequency predicted by the density-dependent hypothesis was not realized the following year (see also Conrad & Pritchard 1989).

Andromorphic *E. boreale* in my Michigan population were only half as common as in a Canadian population of the same species studied by Forbes (1994). This geographical difference in morph frequency could result either from random genetic drift or from a selective advantage gained by andromorphs in the Canadian population. If morph frequencies are determined by natural selection, then experimentally changing the frequencies of an isolated population should result in the eventual return to pre-experimental conditions (e.g. Barker & East 1980), whereas the null hypothesis predicts such changes should persist, assuming no immigration, emigration, or drift occurs.

CONCLUSIONS

Because I failed to find any differences between morphs in fitness trade-offs, and I found no density-, frequency-, or sex ratio-dependent fitness costs or benefits to morphs despite variation in male density, morph frequency and operational sex ratio, my data are consistent with the null hypothesis that female colour morphs in these Michigan populations of *E. hageni* and *E. boreale* are neutral characters with respect to the fitness of sexually mature females.

Although an adaptive value of female dimorphism was not demonstrated in these lifetime studies of coenagrionid damselflies, such colour polymorphism may be adaptive in other populations or species. For example, gene flow via immigrating tenerals from populations where one morph did have some selective advantage might counter any tendency towards random fixation of a morph in my study populations. Alternatively, significant but subtle selective

advantages of the polymorphism among populations or over evolutionary time would not be detected from my extensive study at a single site over a few years. Strong evidence against the null hypothesis would demonstrate one or more of the following: (1) trade-offs in fitness correlates between morphs, (2) density-, frequency-, or sex ratio-dependent selection on morphs, (3) a consistent correlation between morph frequency (over a season or a geographical range) and some biotic factor. It is hoped that the data and arguments presented herein will challenge future researchers to collect appropriate and sufficient data necessary to demonstrate an adaptive advantage for this perplexing phenomenon, if one exists.

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REFERENCES

- Barker, J. S. F. & East, P. D. 1980. Evidence for selection following perturbation of allozyme frequencies in a natural population of *Drosophila*. *Nature, Lond.*, **284**, 166–168.
- Bick, G. H. & Bick, J. C. 1965. Color variation and significance of color in reproduction in the damselfly *Argia apicalis* (Say) (Zygoptera: Coenagrionidae). *Can. Entomol.*, **97**, 32–41.
- Bick, G. H. & Hornuff, L. E. 1966. Reproductive behavior in the damselflies *Enallagma aspersum* and *Enallagma exsulans* (Hagen). *Proc. entomol. Soc. Wash.*, **68**, 78–85.
- Conrad, K. F. & Pritchard, G. 1989. Female dimorphism and physiological colour change in the damselfly *Argia vivida* Hagen (Odonata: Coenagrionidae). *Can. J. Zool.*, **67**, 298–304.
- Cordero, A. 1989. Reproductive behaviour of *Ischnura graellsii* (Rambur) (Zygoptera: Coenagrionidae). *Odonatologica*, **18**, 237–244.

- Cordero, A. 1990a. The inheritance of female polymorphism in the damselfly *Ischnura graellsii* (Rambur) (Odonata: Coenagrionidae). *Heredity*, **64**, 341–346.
- Cordero, A. 1990b. The adaptive significance of the prolonged copulations of the damselfly, *Ischnura graellsii* (Odonata: Coenagrionidae). *Anim. Behav.*, **40**, 43–48.
- Cordero, A. 1992. Density-dependent mating success and colour polymorphism in females of the damselfly *Ischnura graellsii* (Odonata: Coenagrionidae). *J. Anim. Ecol.*, **61**, 769–780.
- Córdoba-Aquilar, A. 1992. Comportamiento reproductivo y policromatismo en *Ischnura denticollis* Burmeister (Zygoptera: Coenagrionidae). *Bull. Am. Odonatol.*, **1**, 57–64.
- De Marchi, G. 1990. Precopulatory reproductive isolation and wing colour dimorphism in *Calopteryx splendens* females in southern Italy (Zygoptera: Calopterygidae). *Odonatologica*, **19**, 243–250.
- Fincke, O. M. 1982. Lifetime mating success in a natural population of the damselfly, *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). *Behav. Ecol. Sociobiol.*, **10**, 293–302.
- Fincke, O. M. 1986a. Underwater oviposition, male vigilance, and female multiple mating in a damselfly (Odonata: Coenagrionidae). *Behav. Ecol. Sociobiol.*, **18**, 405–412.
- Fincke, O. M. 1986b. Lifetime reproductive success and the opportunity for selection in a nonterritorial damselfly (Odonata: Coenagrionidae). *Evolution*, **40**, 791–803.
- Fincke, O. M. 1987. Female monogamy in *Ischnura verticalis* Say (Zygoptera, Coenagrionidae). *Odonatologica*, **16**, 129–143.
- Fincke, O. M. 1988. Sources of variation in lifetime reproductive success in a nonterritorial damselfly (Odonata: Coenagrionidae). In: *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (Ed. by T. H. Clutton-Brock), pp. 24–43. Chicago: University of Chicago Press.
- Fincke, O. M. In press. On the difficulty of detecting density-dependent selection on polymorphic females of the damselfly *Ischnura graellsii*: failure to reject the null. *Evol. Ecol.*
- Forbes, M. R. 1991. Female morphs of the damselfly *Enallagma boreale* Selys (Odonata: Coenagrionidae): a benefit for androchromatypēs. *Can. J. Zool.*, **69**, 1969–1970.
- Forbes, M. R. 1994. Tests of hypotheses for female-limited polymorphism in the damselfly, *Enallagma boreale* Selys. *Anim. Behav.*, **47**, 724–726.
- Futuyma, D. J. 1986. *Evolutionary Biology*. Sunderland, Massachusetts: Sinauer.
- Garrison, R. W. 1978. A mark-recapture study of imaginal *Enallagma cyathigerum* (Charpentier) and *Argia vivida* Hagen (Zygoptera: Coenagrionidae). *Odonatologica*, **7**, 223–236.
- Greenwood, J. J. & Elton, R. R. 1979. Analysing experiments on frequency-dependent selection by predators. *J. Anim. Ecol.*, **48**, 271–237.
- Grieve, E. G. 1937. Studies on the biology of the damselfly *Ischnura verticalis* Say, with notes on certain parasites. *Entomologica Am.*, **17**, 121–153.
- Hafernik, J. E. & Garrison, R. W. 1986. Mating success and survival rate in a population of damselflies: results at variance with theory? *Am. Nat.*, **128**, 353–365.
- Hinneking, B. O. N. 1987. Population dynamics of *Ischnura e. elegans* (Vander Linden) (Insecta: Odonata) with special reference to morphological colour changes, female polymorphism, multiannual cycles and their influence on behaviour. *Hydrobiologia*, **146**, 3–31.
- Hilton, D. F. J. 1987. A terminology for females with colour patterns that mimic males. *Entomol. News*, **98**, 221–223.
- Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.*, **91**, 293–320.
- Johnson, C. 1964. The inheritance of female dimorphism in the damselfly *Ischnura damula*. *Genetics*, **49**, 513–519.
- Johnson, C. 1966. Genetics of female dimorphism in *Ischnura demorsa*. *Heredity*, **21**, 453–459.
- Johnson, C. 1975. Polymorphism and natural selection in *Ischnuran* damselflies. *Evol. Theory*, **1**, 81–90.
- Mook, J. H., Mook, L. J. & Heikens, H. S. 1960. Further evidence for the role of searching images in the hunting behavior of titmice. *Archs néerl. Zool.*, **13**, 448–465.
- Oppenheimer, S. D. & Waage, J. K. 1987. Hand-pairing: a new technique for obtaining copulations within and between *Calopteryx* species (Zygoptera: Calopterygidae). *Odonatologica*, **16**, 291–296.
- Parr, M. J. 1969. Population studies of some Zygopteran dragonflies (Odonata). Ph.D. thesis, University of Salford, U.K.
- Paulson, D. R. 1973. Predator polymorphism and apostatic selection. *Evolution*, **27**, 269–277.
- Paulson, D. R. 1974. Reproductive isolation in damselflies. *Syst. Zool.*, **23**, 40–49.
- Pietrewicz, A. T. & Kamil, A. C. 1981. Search images and the detection of cryptic prey: an operant approach. In: *Foraging Behavior: Ecological, Ethological and Psychological Approaches* (Ed. by A. C. Kamil & T. D. Sargent), pp. 311–331. New York: Garland Press.
- Robertson, H. M. 1985. Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*: females mimicking males. *Anim. Behav.*, **33**, 805–809.
- SAS. 1988. *SAS/STAT User's Guide*. Release 6.03 edn. Cary, North Carolina: SAS Institute.
- Stamps, J. A. & Gon, S. M., III. 1983. Sex-biased pattern variation in the prey of birds. *A. Rev. Ecol. Syst.*, **14**, 231–253.
- Thompson, D. J. 1989. Lifetime reproductive success of andromorph females of the damselfly *Coenagrion puella* (L.) (Zygoptera: Coenagrionidae). *Odonatologica*, **18**, 209–213.
- Tillyard, R. T. 1917. *The Biology of Dragonflies*. London: Cambridge University Press.
- Tinbergen, L. 1960. The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by song-birds. *Archs néerl. Zool.*, **13**, 265–336.

Vane-Wright, R. I. 1980. A classification of sexual interactions, and the evolution of species-specific coloration in butterflies. *Nota lepid.*, 3, 91-93.

Vane-Wright, R. I. 1984. The role of pseudosexual selection in the evolution of butterfly colour patterns. In: *The Biology of Butterflies: Symposium of the Royal*

Entomological Society of London No. 11 (Ed. by R. I. Vane-Wright & P. R. Ackery), pp. 251-253. London: Academic Press.

Walker, E. M. 1953. *The Odonata of Canada and Alaska. Vol. 1*. Toronto: University of Toronto Press.